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Changes in the biodiversity of a deciduous forest ecosystem caused by an increase in the Sika deer population at Ashiu, Japan

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ABSTRACT The deciduous forest of Ashiu, western Japan, the only unspoiled lowland forest ecosystem remaining in the Kinki district, harbors a diverse suite of characteristic flora and fauna. The recent increase in the population of Sika deer (*Cervus nippon*) has greatly impacted the unique forest-floor vegetation. From the 1980s to 2003, we monitored changes in (1) forest understory vegetation, (2) riparian vegetation, (3) roadside vegetation, (4) pollinator visits to flowers, and (5) abundance of leaf-miners. In an *Aesculus*-dominated site, the vegetation of the understory, which had been characterized by diverse perennials in 1987, was replaced by a monotonic stand of the deer-repellent fern *Arachniodes standishii* by 2003, and subendemic plants such as *Cacalia peltifolia* and *Cirsium ashiuense* are now locally extinct. Riparian vegetation, which had been dominated by *Salix gracilistyla* and *Phragmites japonica*, accompanied by diverse perennials in the 1990s, was replaced by sparse stands of deer-repellent *Pterostyrax hispida* and *Clerodendrum trichotomum* by 2003. The species-rich roadside vegetation has also been influenced, and most of the once common herbaceous plants have disappeared. In addition to the decline of herbaceous plants, drastic decreases in the numbers of foraging bumblebees and tephritid leaf-miners were observed in 2003. These results suggest that the population increase of Sika deer has caused reduced populations of pollinators and herbivores through a drastic reduction of their host herbaceous plants between 1990 and 2003, and that control of the Sika deer population by hunting or trapping is urgently required.

KEY WORDS Sika deer / deer browsing / effect of herbivory / pollinator / leaf-miner / Ashiu

Introduction

The Sika deer (*Cervus nippon*), the largest herbivorous mammal in the forests of Japan, was one of the most important prey species of traditional Japanese hunters until the 1940s. Deer meat was harvested, predominantly in autumn, and the fur of this species was used for manufacturing purses and boots (Nishimura, 2003); the leg fur was especially prized for snowshoes, the heel of which was made from the knee of the deer (Matsuyama, 1977). However, demand for the meat and hide of Sika deer began to decrease after the 1950s, due to an increasing supply of industrial products and meat from livestock; subsequently, the number of deer hunters decreased. Accompanied by the extinction of their only natural predators, i.e., Japanese wolves (*Canis lupus hodophilax* and *C. lupus hattai*), deer populations began to increase.

Severe impacts on vegetation resulting from increased herbivory by Sika deer have recently been reported in various localities in Japan (Takatsuki, 1980; Takatsuki, 1989; Takatsuki and Gorai, 1994; Akashi and Nakashizuka, 1999; Nomiya et al., 2002). In the

Nikko area of central Japan, deer browsing has most severely damaged dwarf bamboo and tree seedlings in an *Ulmus*-dominated riparian deciduous forest (Nomiya et al., 2002). Heavy browsing of canopy-tree seedlings restrains the regeneration processes of forests and may ultimately cause the demise of forest ecosystems.

In western Japan, the population levels of Sika deer have been increasing since the 1970s, and high deer densities have caused damage to agriculture and forestry since the 1980s (Sakata et al., 2001). The reported damage to agriculture suggests that the increased Sika deer numbers are affecting the forest-floor vegetation of natural forests around cultivated fields.

The Kyoto University forest at Ashiu, the last natural lowland deciduous forest in the Kinki district, is known for its rich flora of subendemic herbaceous plant species that are confined to the area around Wakasa Bay, e.g., *Cirsium ashiuense, Mitella acerina,* and *Arisaema amurense* ssp. *robustum* var. *ovale* (Okamoto, 1930; Nakai, 1941; Yokoyama et al., 1996; Yasuda and Nagamasu, 1999). As is the case in many forests in Japan, the forest at Ashiu is currently experiencing drastic increases in Sika deer numbers. It is feared that deer browsing may cause local extinctions of subendemic herbaceous understory plants at Ashiu. To assess the impacts of deer browsing, it is necessary to identify the original vegetation that has not been subject to heavy browsing. In a field survey of the flower-visitor community from spring to autumn, Kato et al. (1990) observed the flora, vegetation, and population density of bumblebees and leaf-miners at various sites at Ashiu from 1983 to 1986. These data, though fragmentary, are invaluable for identifying changes in this ecosystem over time.

The objective of this study was to detect the effects of deer browsing on (1) forest understory vegetation, (2) riparian vegetation, (3) roadside vegetation, (4) pollinator visits to flowers, with a special focus on bumblebees, and (5) abundance of leaf-miners. By integrating the observed critical changes with respect to various aspects of the ecosystem, we discuss whether the deer population should be artificially controlled.

Materials and Methods

The Kyoto University forest at Ashiu is located near Wakasa Bay (35°19'N, 135°45'E) at an altitude ranging from 355 to 959 m. This area experiences heavy snow fall in winter, and deep snow has caused high mortality of Sika deer in unusually cold years. There are three types of forest: (i) beech forest dominated by *Fagus crenata*, which is characteristically accompanied by *Cryptomeria japonica*, (ii) deciduous oak forest dominated by *Quercus mongolica* and accompanied by *Q. salicina* and *Carpinus* spp., and (iii) riparian forest dominated by *Aesculus turbinata*, *Cercidiphyllum japonicum*, and *Pterocarya rhoifolia*. About half of the University forest is maintained as a protected area (Fig. 1).

(1) Forest floor vegetation in the Tochi-dani Valley

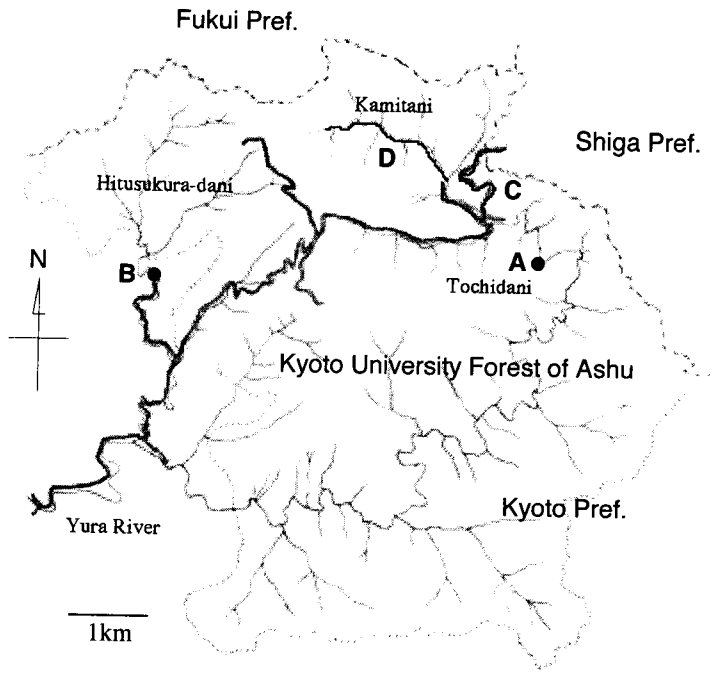

Fig. 1. Map of the Kyoto University Forest at Ashiu, showing location of the study sites: A, the Tochi-dani site where forest floor vegetation was monitored; B, the Hitsukura-dani site where riparian vegetation was monitored; C, the road at Kamitani where roadside vegetation and tephritid leaf-miner community were monitored; D, the Kamitani trail along which pollinator visits to flowers were monitored.

The site where the Tochi-dani meets the Yura River (Fig. 1A) is a riparian forest dominated by large *Aesculus turbinata*; in the 1980s, the forest understory at this site was inhabited by subendemic perennials such as *Cacalia peltifolia* and *Cirsium ashiuense*. We surveyed the forest floor vegetation at the entrance of the valley on 27 September 1987 and 2 September 2003, and the coverage of each plant species was recorded as follows: 1, 0–25; 2, 25–50; 3, 50–75; 4, 75–100; 5, 100 % coverage; +, rare appearance. Photographs taken during each survey aided in the comparison of vegetation profiles between 1987 and 2003.

(2) Riparian vegetation in the Hitsukura-dani Valley

The Hitsukura-dani Valley is a tributary of the Yura River and was initially covered by riparian vegetation dominated by *Salix gracilistyla* and *Phragmites japonica*. The riparian vegetation at site B in Fig. 1 was surveyed on 24 August 1992 and 2 September 2003, and the coverage of each plant species (as described above) was compared between surveys.

(3) Roadside vegetation at Kamitani

Kamitani is the central part of the protected area, and the roadside vegetation around Choujidani is characterized by native plants growing in sunny habitats. The roadside vegetation along route C in Fig. 1 was surveyed on 24 September 1986, 19 October 1999, and 2 September 2003, and the coverage of each plant species was compared between surveys.

(4) Pollinator visits to flowers at Kamitani

Field censuses of the anthophilous insect community were conducted from 1983 to 1986 along trail D in Fig. 1. In these censuses, we walked along the trail to find flowers, and upon encountering flowers, we collected all flower visitors for 10 minutes (Kato et al., 1990). For flower visitors in autumn, we collected data on 2 October 1983, 24 September 1984, 15 September 1985, and 24 September 1986. All flowers blooming in autumn were on herbaceous plants, and the most dominant flower visitors were bumblebees. We conducted additional similar surveys on 28 September 1987, 12 September 1993, and 2 September 2003. We compared bumblebee and honeybee visits to 15 different species of flowers in the surveys undertaken from 1983 to 2003.

(5) Abundance of leaf-miners at Kamitani

Larvae of some tephritid flies are leaf-miners of plants in the families Asteraceae, Apiaceae, and Verbenaceae. We observed the presence or absence of six species of tephritid leaf-miners on these host plants along trail C in Fig. 1 on 24 September 1984, 19 October 1999, and 2 September 2003.

Results

(1) Forest-floor vegetation

In 1987, the forest understory in the *Aesculus*-dominated forest at Tochi-dani was rich in herbaceous plants (Plate 6A, Table 1). By 2003, the species-rich forest floor vegetation had been replaced by a nearly homogeneous stand of the fern *Polystichum tripteron* (Plate 6B, Table 1). The total number of understory plant species decreased from 20 to five. Most shrubs and herbaceous perennials, including *Cacalia peltifolia* and *Cirsium ashiuense*, became extinct at this site. Near the site, characteristic stands of dwarf bamboo, *Sasa kurilensis*, and the creeping shrub, *Cephalotaxus harringtonia*, were stunted or almost killed as a result of heavy browsing by deer.

The plant species that were originally rare and have recently obviously declined are *Cacalia peltifolia, Rodgersia podophylla, Arnica mallatopus, Veronica japonensis, Pyrola japonica, Chelonopsis moschata*, and *Euonymus lanceolatus*. In contrast, plants that were damaged very little by deer browsing were *Arachniodes standishii, Dryopteris crassirhizoma, Polystichum tripteron, Arachniodes mutica, Clerodendrum trichotomum, Pterostyrax hispida, Symplocos chinensis*, and *S. coreana*.

Table 1. Changes of vegetation of forest understory at Tochi-dani valley at Ashu from 1987 to 2003.

Plant species	Family	Habit[1]	Coverage 1987	Coverage 2003
Arachniodes standishii	Dryopteridaceae	p	3	4
Cephalotaxus harringtonia var. *nana*	Cephalotaxaceae	s	2	
Elatostema umbellatum var. *majus*	Urticaceae	p	2	
Dryopteris crassirhizoma	Dryopteridaceae	p	1	1
Polystichum tripteron	Dryopteridaceae	p	1	1
Boehmeria tricuspis	Urticaceae	p	1	
Persicaria debilis	Polygonaceae	p	1	
Reynoutria japonica	Polygonaceae	p	1	
Hydrangea serrata var. *megacarpa*	Hydrangeaceae	s	1	
Cardiandra alternifolia	Hydrangeaceae	p	1	+
Chrysosplenium fauriei var. *kiotense*	Saxifragaceae	p	1	
Euonymus alatus f. *stiatus*	Celastraceae	s	1	
Angelica polymorpha	Apiaceae	p	1	
Cacalia peltifolia	Asteraceae	p	1	
Cirsium ashiuense	Asteraceae	p	1	
Laportea bulbifera	Urticaceae	p	+	
Hydrangea petiolaris	Hydrangeaceae	l	+	+
Viola vaginata	Violaceae	p	+	
Aralia cordata	Apiaceae	p	+	
Salvia glabrescens	Lamiaceae	p	+	

[1] p, perennial; s: shrub; l, liana.

(2) Riparian vegetation

In 1992, the riparian vegetation at site B in the Hitsukura-dani Valley was dominated by *Salix gracilistyla* and *Phragmites japonica* and was accompanied by various herbaceous riparian plants such as *Boehmeria tricuspis, Persicaria thunbergii, P. hydropiper* and *P. yokusaiana.* By 2003, the vegetation profile had drastically changed,such that the riparian habitat was almost devoid of vegetation except for sparse stands of

Table 2. Change of riparian vegetation at Hitsukura-dani valley at Ashiu from 1992 to 2003.

Plant species	Family	Habit[1]	Coverage 1992	Coverage 2003
Salix gracilistyla	Salicaceae	s	3	
Weigela hortensis	Caprifoliaceae	s	2	
Phragmites japonica	Poaceae	p	2	1
Boehmeria tricuspis	Urticaceae	p	1	
Reynoutria japonica	Polygonaceae	p	1	
Carex persistens	Cyperaceae	p	1	+
Persicaria hydropiper	Polygonaceae	p	1	
Persicaria thunbergii	Polygonaceae	p	1	
Symplocos chinensis	Symplocaceae	s	1	
Cirsium ashiuense	Asteraceae	p	+	
Persicaria yokusaiana	Polygonaceae	p	+	
Angelica polymorpha	Apiaceae	p	+	
Clerodendrum trichotomum	Verbenaceae	t		1
Pterostyrax hispida	Styracaceae	t		2

[1] p, perennial; s, shrub; t, tree.

Pterostyrax hispida and *Clerodendrum trichotomum* (Plate 6C, Table 2). Upstream along the Hitsukura-dani Valley, we found that native streamside vegetation, which was composed of various riparian plants (*Hosta sieboldiana, Mitella acerina*, and *Elatostema umbellatum* var. *majus*), remained on a wet steep slope where deer could not reach.

(3) Roadside vegetation

Table 3. Changes of roadside vegetation at Kaimatani from 1986 to 2003.

Plant species	Family	Habit[1]	Coverage		
			1986	1999	2003
Sasa kurilensis	Poaceae	s	2	1	+
Weigela hortensis	Caprifoliaceae	s	2	1	+
Hydrangea hirta	Hydrangeaceae	s	1	1	+
Hydrangea serrata var. *megacarpa*	Hydrangeaceae	s	1	+	
Hydrangea paniculata	Hydrangeaceae	s	1	1	+
Deutzia crenata	Hydrangeaceae	s	1	1	+
Miscanthus sinensis	Poaceae	p	1	+	+
Boehmeria tricuspis	Urticaceae	p	1	1	
Petasites japonicus	Asteraceae	p	1	1	
Adenocaulon himalaicum	Asteraceae	p	1	1	+
Artemisia princeps	Asteraceae	p	1	1	
Kalimeris yomena	Asteraceae	p	1	1	
Anthriscus aemula	Apiaceae	p	1	+	
Reynoutria japonica	Polygonaceae	p	1	+	
Persicaria thunbergii	Polygonaceae	p	1	+	+
Aster glehni var. *hondoensis*	Polygonaceae	p	1	+	
Euonymus alatus f. *stiatus*	Celastraceae	s	1	1	+
Agrimonia pilosa var. *japonica*	Rosaceae	p	1	1	+
Geum japonicum	Rosaceae	p	1	+	
Rubus palmatus	Rosaceae	s	1	1	
Salix gracilistyla	Salicaceae	s	+	+	
Pterostyrax hispida	Styracaceae	t	+	+	1
Cirsium ashiuense	Asteraceae	p	+		
Aster ageratoides ssp. *Ovatus*	Asteraceae	p	+	+	
Eupatorium chinense	Asteraceae	p	+	+	
Clerodendrum trichotomum	Verbenaceae	t	+	+	1
Lysimachia clethroides	Primulaceae	p	+		
Isodon trichocarpa	Lamiaceae	p	+		
Isodon longituba	Lamiaceae	p	+	+	
Clinopodium gracile	Lamiaceae	p	+	+	
Viola kusanoana	Violaceae	p	+	+	
Angelica pubescens	Apiaceae	p	+	+	
Angelica polymorpha	Apiaceae	p	+	+	
Persicaria yokusaiana	Polygonaceae	p	+	+	
Persicaria trigonocarpa	Polygonaceae	p	+	+	
Antenoron filiforme	Polygonaceae	p	+	+	+
Impatiens textori	Balsaminaceae	a	+	+	
Ampelopsis brevipedunculata	Vitaceae	c	+	+	
Astilbe thunbergii	Saxifragaceae	p	+		

[1] a, annual; c, climber; p, perennial; s, shrub.

At Kamitani, roadside vegetation was originally characterized by native herbaceous plants belonging to the Asteraceae, Lamiaceae, Apiaceae, Urticaceae, and Poaceae. The edible herb *Petasites japonicus*, which was abundant along roadsides, was collected by local people in the 1980s. However, this roadside plant disappeared between the 1980s and 2003 (Table 3). The plant species that were once common but have almost disappeared from roadsides are *Petasites japonicus, Artemisia princeps, Aster glehni* var. *hondoensis, Miscanthus sinensis, Boehmeria tricuspis, Persicaria thunbergii, Isodon trichocarpa*, and *Angelica polymorpha*. The only species surviving along roadsides in this area is *Clerodendrum trichotomum*.

(4) Pollinator visits to flowers

Although the flora in Ashiu had initially supported a rich pollinator fauna (Kato et al., 1990), the drastic decrease in herbaceous plants in and around the forest has caused a concurrent decrease in populations of anthophilous insects. Table 4 shows changes in bumblebee and honeybee visits to autumn-blooming flowers at Kamitani from 1983 to 2003. In autumn throughout the 1980s and 1990s, two bumblebee species, *Bombus diversus* and *B. honshuensis*, were commonly observed on 14 species of flowers that were particularly abundant along streams, trails, and roadsides. In 1993, bumblebee and

Table 4. Records of bee visits to autumn flowers at Kamitani from 1983 to 2003: +, visits observed; -, no visit observed; n, no flowers found.

Visitor species / Flower species	Visits						
	1983	1984	1985	1986	1987	1993	2003
Bombus diversus							
Aconitum sanyoense	-	-	-	-	-	+	-
Persicaria thunbergii	-	+	-	-	-	-	n
Impatiens textori	+	+	+	+	+	+	n
Rabdosia longituba	+	-	+	-	+	+	-
Rabdosia trichocarpa	-	+	-	-	+	+	n
Salvia glabrescens	+	+	-	-	-	+	n
Caryopteris divaricata	-	-	+	+	n	n	n
Chelonopsis moschata	-	-	-	-	-	+	n
Ainsliaea acerifolia	-	-	-	+	-	-	+
Cirsium ashiuense	+	+	-	+	+	-	n
Calanthe reflexa	-	-	-	-	-	+	+
Bombus honshuensis							
Spuriopimpinella nikoensis	-	+	-	-	-	n	n
Rabdosia longituba	+	-	-	-	-	+	-
Rabdosia trichocarpa	+	+	+	+	+	+	n
Salvia glabrescens	-	-	-	-	-	+	n
Cacalia delphiniifolia	-	+	-	-	-	+	n
Cirsium ashiuense	+	-	+	+	+	-	n
Calanthe reflexa	-	-	-	-	-	+	-
Bombus hypocrita							
Angelica pubescens	-	-	-	-	-	+	n
Apis cerana							
Isodon trichocarpa	-	+	+	+	+	-	n

honeybee visits to the flowers of *Cirsium ashiuense* and *Isodon trichocarpa*, respectively, were not observed, whereas bumblebee visits to other herbaceous flowers were still recorded. On 2 September 2003, we found only one individual bumblebee (*Bombus diversus*), which visited *Ainsliaea acerifolia*. This bumblebee had three pairs of pollinia of *Calanthe reflexa* on its head, suggesting that it may have visited various flowers that are now rare. It is likely that the disappearance of autumn-blooming herbaceous plants of the Asteraceae and Lamiaceae has affected the density of these apid bees.

(5) Abundance of leaf-miners

Tephritid leaf-miners mine the palisade parenchyma of host-plant leaves and then pupate in the soil. At Kamitani (along trail C in Fig. 1), we found six tephritid leaf-miner species on nine plant species in 1986. In 2003, however, we found only one species mining the leaves of *Clerodendrum trichotomum* (Table 5). This result suggests that the drastic decrease in herbaceous plants caused local extinctions of five tephritid species associated with the herbaceous plants.

Table 5. Records of tephritid leafminers observed on their host plants at Kamitani from 1986 to 2003: +, leaf-miners observed; -, no leaf-miner observed; n, no plant found.

Tephritid species	Host plant species	Family	Records		
			1986	1999	2003
Parahypenidium polyfasciatum	*Clerodendrum trichotomum*	Verbenaceae	+	+	+
Prionimera japonica	*Petasites japonicus*	Asteraceae	+	+	-
Shiracidia s-nigrum	*Cirsium ashiuense*	Asteraceae	+	-	n
Stenomocera montivaga	*Kalimeris yomena*	Asteraceae	+	+	n
	Aster glehni var. *hondoensis*	Asteraceae	+	+	n
	Aster ageratoides ssp. *Ovatus*	Asteraceae	+	+	-
	Eupatorium chinense	Asteraceae	+	+	n
Trypeta artemisiae	*Artemisia princeps*	Asteraceae	+	+	-
Yamanowotome accepta	*Angelica pubescens*	Apiaceae	+	-	n

Discussion

The results of our long-term surveys suggest that the forest understory vegetation, riparian vegetation, and roadside vegetation have been drastically degraded, most likely because of intense browsing by deer. Although quantitative data are lacking, deer density has greatly increased over the last ten years at Ashiu. Deer feces are readily found, even along the road in the forest. In Hyogo Prefecture, west of Kyoto Prefecture, the deer density is so high that serious damage to agriculture and forestry has been reported since the 1980s (Sakata et al., 2001). In the natural forest at Ashiu, deer browsing has caused decreases in almost all understory plant species except for deer-repellent plant species such as *Arachniodes standishii*, *Clerodendrum trichotomum*, and *Pterostyrax hispida*. The latter two species, which were uncommon before the 1980s, are now abundant in Ashiu.

Deer browsing not only affects forest regeneration, but it also reduces the diversity

of herbaceous plant species. Frequently-browsed perennials are killed if deer browsing continues over several years. Thus, several subendemic plant species, including *Cacalia peltifolia* and *Cirsium ashiuense*, are now critically endangered due to browsing in Ashiu. Some perennials, such as *Cirsium ashiuense*, overwinter as rosettes, which are subject to severe browsing, particularly in warm winters without deep snow cover.

The recent increase in deer populations also suggests that deer have potentially affected the wide-scale distribution of plants. Japan has 27 endemic plant genera, of which five (*Ancistrocarya, Diaspananthus, Miricacalia, Hakonechloa,* and *Alectorurus*) are confined to riparian habitats along steep-sided rocky valleys in southwestern Japan (Murata, 1977). In addition to these endemic genera, the distributions of many endemic herbaceous species are confined to the Sohayaki area, i.e., the area covering Kyushu, Shikoku, and the Kii Peninsula. As steep rocky slopes along valleys are refugia for these herbaceous plants under heavy browsing pressure, the restricted distribution of these endemic riparian herbaceous species may have been determined by historical outbreaks of Sika deer during the Quaternary.

The riparian vegetation formerly dominated by *Salix gracilistyla* and *Phragmites japonicus* has disappeared in recent years (Table 2). The edible riparian plant *Elatostema umbellatum* var. *majus*, which was once harvested by local people, is now rare in Ashiu. The disappearance of riparian vegetation may cause erosion of stream banks after heavy rains, and the structural changes of river beds may negatively influence river salmon *Salmo (Oncorhynchus) masou masou* and the giant aquatic salamander *Megalobatrachus japonicus.*

Although it was rare in the 1980s to encounter deer in the forest, they are now easily observable, even on roads in the forest. As a result, the once rich roadside vegetation has disappeared in recent years (Table 3). Sika deer are reported to prefer herbaceous plants such as *Artemisia* and *Miscanthus* (Matsuyama, 1977), and this coincides with the drastic disappearance of herbaceous plants in the families Asteraceae and Poaceae.

The results in Table 4 suggest that the increased deer density has indirectly caused a decrease in anthophilous insect populations, especially bumblebees, in autumn. Drastic decreases in autumn-flowering herbaceous plants have caused significant decreases in floral resources for bees. At Kamitani, flowers of the Asteraceae and Lamiaceae were abundant and diverse in the 1980s and were visited by many bumblebees (Kato et al., 1990). In the fall of 2003, however, flowers were very rare, and only one bumblebee was observed. The bumblebee did not major its flower species because there were no herbaceous plant species bearing abundant flowers. Arboreal flowers remain available that can foster bumblebees from spring to early summer; after midsummer, however, trees or shrubs no longer flower, i.e., only herbaceous plants flower after midsummer (Kato et al., 1990). Accordingly, the decrease in autumn-flowering herbaceous plants will severely affect the bumblebee population, especially because most bumblebee species, except *Bombus ardens*, produce reproductives in the fall. A decrease in bumblebee reproductives in the fall will likely cause a decline in the number of bumblebee colonies in the following spring, thereby reducing the pollination success of bumblebee-pollinated flowers.

The reduction of herbaceous plants caused decreases or local extinctions of tephritid leaf-miners associated with host plants in the Asteraceae and Apiaceae. At Kamitani, we found only one tephritid species in 2003, which mined the leaves of the deer-repellent shrub *Clerodendrum polyfasciatum*. These results suggest that the decrease in available host plants has directly caused a decrease in herbivore populations. Due to drastic reductions in *Cirsium ashiuense*, the herbivorous coccinelid beetle *Henosepilachna pustulosa*, which was abundant in the 1970s (Nakamura and Ohgushi, 1979), has become almost extinct at Kamitani. In addition to these direct effects on herbivorous insects, deer browsing sometimes increases leaf hardness, which exerts an indirect negative effect on herbivorous insects (Shimazaki and Miyashita, 2002).

Thus, deer browsing has not only reduced herbaceous plants and seedlings of canopy trees, but it has also indirectly caused a decrease in pollinator and herbivore populations, and has ultimately altered the ecosystem at Ashiu. We conclude that the deer population should be managed by hunting or trapping in order to conserve the biodiversity of plants, pollinators, and herbivores. The management policy for Sika deer has been described by Matsuda et al. (1999), and the utility of this policy has been confirmed by the deer management in Hyogo Prefecture (Sakata et al., 2001). Beech forests are known to regenerate when dwarf bamboo stands decline under temporal but not excessive pressure by browsing vertebrates (Nakashizuka and Numata, 1982). Urgent control of the deer population at Ashiu will contribute to the conservation of a rich understory flora and to the regeneration of the beech forest.

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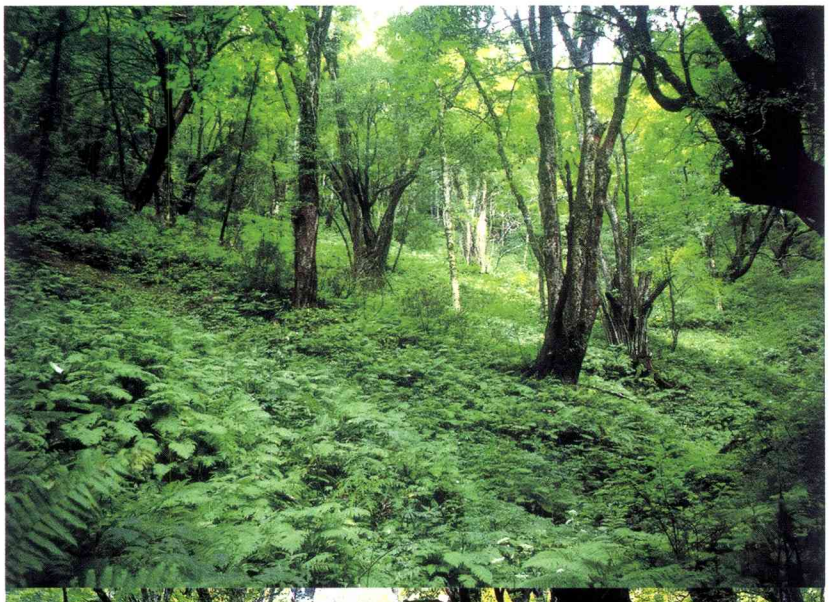
Plate 6. Changes of vegetation at Ashiu

A–B, Landscape of the Tochi-dani Valley site on 27 September 1987 (A) and 2 September 2003 (B). The lush vegetation accompanied by diverse herbaceous plants observed in 1987 had disappeared by 2003. **C**, Landscape of a riparian habitat at Hitsukura-dani on 2 Sept. 2003. The stands of *Phragmites japonica* and *Salix gracilistyla* were replaced by a sparse stands of *Clerodendrum trichotomum* and *Pterostyrax hispida*.

A



B

C